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Limitations of invasive snake control tools in the context of a new invasion on an island with abundant prey

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Abstract

In October 2020, a new population of invasive brown treesnakes (*Boiga irregularis*) was discovered on the 33-ha Cocos Island, 2.5 km off the south coast of Guam. Cocos Island is a unique conservation resource, providing refuge for many lizards and birds, including endangered species, which were extirpated from mainland Guam by invasive predators including brown treesnakes. We sought to evaluate the usefulness of toxic baiting with acetaminophen-treated carrion baits and cage trapping, common tools for the control of brown treesnakes on mainland Guam, as potential eradication tools on Cocos Island. We evaluated multiple bait types and bait presentations: on the ground, suspended in the canopy emulating aerial bait applications and in four plastic-tube bait station configurations intended to exclude non-target species. We monitored all baits with time-lapse cameras. Despite improved exclusion of non-targets by bait station design, most baits were quickly removed by non-target species, particularly coconut crabs (*Birgus latro*) and Mariana monitors (*Varanus tsukamotoi*). Monitoring of 1,250 baits available for 2,427 bait nights resulted in no observations of brown treesnakes taking any bait. Subsequently, we tested two trap types commonly used on Guam and compared trapping success with live versus dead mouse lures. In 10,553 trap nights using live and dead mouse lures, we only captured one brown treesnake, in a trap with a live mouse

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lure. These baiting and trapping rates are so low as to be ineffectual for all practical purposes. Concurrent visual searching and hand capture of brown treesnakes during initial rapid response efforts demonstrates that these low baiting and trapping success rates are not a result of low snake density. We make a case for our assumption that the ineffectiveness of these tools on Cocos Island is due to the context of extremely high abundance of preferred live prey, primarily large geckos and birds. Our results have profound conservation ramifications, because any future island invasions by brown treesnakes are likely to occur within similarly prey-rich environments where these baiting and trapping methods might be similarly ineffective.

Keywords

bait stations, *Boiga irregularis*, camera traps, conservation, eradication feasibility, incipient population, non-target species, trapping

Introduction

The pace and scale of the introduction and spread of non-native reptiles continues to increase, as does recognition of the attendant ecological and economic harms they cause (Kraus 2009; Reed and Kraus 2010; Kraus 2015; Capinha et al. 2017). Snakes comprise a considerable proportion of these reptile invasions, many of which occur on islands where already-imperilled native species are at risk of extirpation or extinction by snake predation; examples include wolf snakes (*Lycodon aulicus*) on Mauritius and Réunion Island (Deso and Probst 2007), corn snakes (*Pantherophis guttatus*) and boa constrictors (*Boa constrictor*) on multiple Caribbean islands, California kingsnakes (*Lampropeltis californiae*) in the Canary Islands and multiple colubrids in the Balearic Islands (Tonge 1990; Perry et al. 2003; Bushar et al. 2015; Monzón-Argüello et al. 2015; Silva-Rocha et al. 2015). Invasive snake problems can be particularly intractable because of snakes' cryptic nature and ability to withstand long periods without feeding (Durso et al. 2011; Siers et al. 2018a; Yackel Adams et al. 2018; Boback et al. 2020; Nafus et al. 2020). To date, there are no known examples of eradication of an invasive snake population at a scale larger than 1 ha (Campbell et al. 2012; DIISE 2023).

The most well-known and well-studied example of an island snake invasion is that of the brown treesnake (*Boiga irregularis*) on the island of Guam in the Western Pacific. Accidentally transported from the Admiralty Islands to Guam in shipments of military equipment following World War II (Rodda and Savidge 2007; Richmond et al. 2015), this slender, nocturnal, arboreal predator spread throughout the entire island by the mid-1980s (Savidge 1987) and achieved densities unprecedented for any natural non-aggregating snake population (Rodda et al. 1999a). The spread of brown treesnakes across Guam was followed by a wave of negative impacts to all native vertebrate taxa (Wiles 1987; Fritts and Rodda 1998) including collapses in nearly all native bird populations, resulting in the extirpation or extinction of 12 of 15 native forest birds and the functional extinction of the island's entire forest avifauna (Savidge 1987; Wiles et al. 2003). This bird loss was followed by cascading effects on plants, invertebrates and ecological processes (Perry and Morton 1999; Rogers et al. 2012;

Caves et al. 2013; Fricke et al. 2014; Freedman et al. 2018). Socioeconomic damages caused by the brown treesnake invasion of Guam include 'home invasions' and painful bites to humans including infants (Fritts 1988; Fritts et al. 1990, 1994), predation on domestic animals including the loss of small-scale poultry production (Fritts and McCoid 1991; Rodda and Savidge 2007), declines in tourism (Hall 1996; Shwiff et al. 2010) and costs of power outages caused by snakes short-circuiting transmission lines (Fritts 2002).

Methods and strategies for brown treesnake control are being developed, tested and implemented for the protection and restoration of Guam's native flora and fauna (e.g. Aguon et al. (2002); Siers et al. (2017a, 2020a, b); Clark et al. (2018); Klug et al. (2021a, b); Pollock et al. (2021)). However, the first and highest priority for invasive brown treesnake control has been interdiction–the prevention of further spread of this harmful predator from Guam to other vulnerable locations throughout the Pacific (Hall 1996; Stanford and Rodda 2007; Perry and Vice 2009; Clark et al. 2018; Engeman et al. 2018). The Commonwealth of the Northern Mariana Islands (CNMI, especially Saipan, Rota and Tinian) and the Hawaiian Archipelago are at particularly high risk of invasion and severe ecological and economic consequences (Fritts 1988; Shwiff et al. 2010; BTSTWG 2015; Yackel Adams et al. 2021). Before the implementation of a full interdiction programme on Guam, live brown treesnakes were too-commonly found in cargo from Guam to Saipan, Hawaii and other destinations; since a USDA Wildlife Services operational control programme began in 1993, such encounters have dropped to nearly zero and Saipan continues to be considered snake-free (Hall 1996; Stanford and Rodda 2007; Yackel Adams et al. 2018, 2021).

Cocos Island (CHamoru name: Islan Dåno') is a small atoll island situated approximately 2.5 km off the southern tip of the main island of Guam. Cocos Island was considered to comprise the majority of remaining snake-free habitat in Guam and is home to many vertebrates susceptible to brown treesnake predation, including some species that no longer persist on mainland Guam. Guam rails (*Hypotaenidia owstoni*: ko'ko'), once extinct in the wild due to brown treesnake predation, were introduced to Cocos Island where they have reproduced and thrived (Medina and Aguon 2000). The endangered Mariana skink (*Emoia slevini*) was extirpated from mainland Guam by brown treesnake predation, but a remnant population was recently rediscovered on Cocos Island (USFWS 2019). Other species, including regionally endemic lizards and birds, also persist on Cocos Island (Rodda and Fritts 1992).

While the high volume of commercial and military cargo and vessels originating from central and northern Guam has been scrupulously inspected for stowaway snakes, traffic between southern Guam and Cocos Island has received relatively little attention. A biosecurity plan was developed for the Island (USDA Wildlife Services 2009) to monitor for incursions of cats, rodents and snakes on Cocos Island, as well as control snakes in high traffic areas, i.e. vessels that visited Cocos Island daily for business. An awareness campaign targeted staff and visitors to Cocos Island to report sightings and conduct boat inspections. The implementation of personal craft inspections was voluntary with no regulatory enforcement.

In October 2020, a local fisherperson reported killing snakes on Cocos Island during a night-time visit to the atoll. Subsequent search efforts by the U.S. Geological Survey's (USGS) Brown Treesnake Rapid Response Team (RRT; Stanford and Rodda 2007) confirmed a population of brown treesnakes on Cocos Island (Guam Department of Agriculture 2020; Barnhart et al. 2022). The RRT intermittently continued night-time searches through September 2021, with additional training exercises ongoing through September 2023 and had sighted 64 brown treesnakes (58 of which were captured and euthanised; U.S. Geological Survey 2023). As of September 2023, the volunteer group Friends of Islan Dåno had captured and removed 36 brown treesnakes (Martin Kastner, Friends of Islan Dåno, written communication, 2023) and USDA Wildlife Services had removed an additional 23 (Alyssa Taitano, USDA, written communication, 2023). Currently, these search and removal efforts continue intermittently while agencies plan for a more comprehensive response, potentially including an eradication effort (USDA Wildlife Services 2021a, b). Preliminary USGS data reflect an apparently reproductive population, with representatives of all size classes captured and much larger and heavier snakes than found in similar samples from Guam (Barnhart et al. 2022).

Several tools and techniques have been developed and continue to be improved for management of invasive brown treesnakes on Guam (Clark et al. 2018). The common human pharmaceutical acetaminophen (paracetamol) has been identified as an effective oral toxicant for brown treesnakes (Savarie et al. 2000; Siers et al. 2021) with a relatively low environmental risk profile (Johnston et al. 2002). A tablet containing 80 mg of acetaminophen has been registered with the U.S. Environmental Protection Agency as a vertebrate pesticide for brown treesnake control (Reg. No. 56228-34). Coupled with carrion baits (typically 4–6 g dead neonatal mice), acetaminophen baiting has been demonstrated to reduce brown treesnake abundance on a landscape scale (Savarie et al. 2001; Clark and Savarie 2012; Siers et al. 2020a, b), has become a mainstay of interdiction operations (Clark et al. 2012; Clark et al. 2018; Engeman et al. 2018) and is suggested to be capable of eradicating brown treesnakes on Guam within snake barriers, as part of an integrated pest management strategy (Nafus et al. 2022). Baiting can be more cost-effective than traditional trapping methods (Clark et al. 2012) and, as such, was thought to be a desirable eradication tool for managing the established brown treesnake population on Cocos Island.

Since the early 1990s, live trapping with cage traps has been the primary method of brown treesnake removal and continues to be a foundational tool for research and management programmes (Engeman and Linnell 1998; Tyrrell et al. 2009; Clark et al. 2018; Engeman et al. 2018). Current trap designs are modifications of crayfish or minnow traps, composed of a cylindrical wire mesh trap body with a funnel at each end. Stock funnel openings are widened and covered with a wire mesh one-way flap to allow snakes access to the trap body, but blocking escape. A live mouse in a protective chamber is the lure that entices snakes into them. Although these brown treesnake traps are considered the most efficient snake traps in the world (Rodda et al. 1999b), care and provisioning of live mice is costly and infrared photography has indicated that many snakes that encounter traps fail to enter the trap (Yackel Adams et al. 2019).

Moreover, as food resources become more abundant, live mouse traps may have decreasing efficacy, which is of potential importance in rapid response settings (Gragg et al. 2007; Stanford and Rodda 2007). Traps are also expensive and prone to damage by non-target species, particularly coconut crabs (*Birgus latro*) and Mariana monitors (*Varanus tsukamotoi* [nee *indicus*]). Due to these drawbacks, trapping is seen as an effective brown treesnake removal tool, but probably with greatest value when integrated with acetaminophen baiting (Nafus et al. 2022).

It is important to conduct pilot evaluations of the utility of potential control tools to establish their effectiveness prior to substantial investments in planning eradication projects (Genovesi 2001; Clout and Williams 2009). Identifying the limitations of control tools is critical for preliminary feasibility assessments and managing eradication costs. Prior to planning for an eradication attempt on Cocos Island, we sought to evaluate the practicality of acetaminophen baiting and live trapping in the context of the Island's prey-rich environment which is similar to possible scenarios if brown treesnakes were to successfully arrive and establish a population in other areas vulnerable to invasion. Our general objectives for both methods were to evaluate: 1) brown treesnake removal rates with various tool implementation methods; 2) interference by non-target species with brown treesnake removal methods; and 3) potential harm to native species from brown treesnake removal methods.

Methods

Study location

Cocos Island (33.6 ha; Fig. 1) is centred at approximately 13.238°N, 144.653°E and located 2.5 km southwest from the southern coast of Guam, forming part of the Merizo Barrier Reef surrounding Cocos Lagoon. The vegetation is described in detail in Fosberg (1960). The substrate is deep, well-drained loamy sand and the flora is primarily *Casuarina equisetifolia* forest in the northeast, while the south-western portion of the island is primarily mixed strand forest comprising *Cocos nucifera*, *Hernandia sonora*, *Guettarda speciosa*, *Merrilliodendron megacarpum*, *Morinda citrifolia*, *Intsia bijuga*, *Casuarina equisetifolia*, *Terminalia catappa*, *Tournefortia argentea*, *Carica papaya*, *Barringtonia asiatica*, *Hibiscus tiliaceus*, *Leucaena leucocephala* and *Thespesia populnea*. Vegetation along the south-eastern shore is dominated by *Pemphis acidula* and *Scaevola sericea*, while the north-western coastline is mostly open sand.

The north-eastern 80% of the Island is under private ownership and the south-western 20% is owned by the Government of Guam and managed by the Guam Department of Parks and Recreation. The Island is uninhabited, but Cocos Island Resort operates as a day resort offering water-sports, trail walks and food and beverages. The resort closed when the Governor of Guam declared an island-wide public emergency shutdown in response to the COVID-19 pandemic on 13 March 2020. The resort has not yet reopened since then.

Figure 1. Map of Cocos Island 2.5 km from the southern tip of Guam, USA. Orange lines indicate locations of trails used for bait applications and trapping. The top of the image is orientated to the north. Image: Maxar Intelligence 2021.

To minimise disturbance of threatened and endangered species present on the Island, our activities were limited to the edges of existing cart paths and footpaths as per the conditions of our U.S. Fish and Wildlife Service Endangered Species Act consultation (Fig. 1). Cart paths and trails on Cocos Island receive very little maintenance or traffic and are primarily under continuous canopy and do not substantially alter the surrounding forest structure. The majority of mainland Guam brown treesnake research is conducted along road edges and maintained transects (e.g. Christy et al. (2010); Siers et al. (2017b)) so we believe it unlikely that limiting activities to these areas would bias results.

Acetaminophen baiting

We sought to evaluate the relative merits of a variety of potential baits and bait presentation methods on Cocos Island. Preliminary evidence from mainland Guam indicates that brown treesnakes with recent experience feeding on birds may be preferentially attracted to dead bird baits over dead rodents (Nafus et al. 2021). To evaluate bait

preferences, we offered three sizes of dead mice and two sizes of dead bird chicks as baits, which where suitable to the presentation method: 4–6-gram dead neonatal mice (DNM); 10–17-g small mice (SM); 18–35-g large mice (LM); 10–14-g small bird baits (hatchling quail, SB); and 25–35-g large bird baits (hatchling chickens, LB) (Fig. 2). All baits were monitored with commercial infrared game cameras (H68, Apeman, Shenzhen, China) set to time-lapse with one image recorded every 30 seconds for 24 hours per day.

Figure 2. Dead animal baits used in this study. Left to right: 4–6-g dead neonatal mouse (DNM); 10–17-g small mouse (SM); 18–35-g large mouse (LM); 10–14-g small bird (quail chick, SB); and 25–35-g large bird (chicken chick, LB).

Canopy presentation: USDA Wildlife Services has engineered an Aerial Delivery System (ADS) for the automated assembly and aerial distribution of bait cartridges containing a DNM treated with a tablet containing 80 mg of acetaminophen (Siers et al. 2019a, 2020b, 2021; Goetz et al. 2020, 2021). These cartridges open upon ejection from the aircraft, exposing a ribbon to cause entanglement in the forest canopy where arboreal treesnakes forage, preventing baits from falling to the forest floor where they can be taken by terrestrial non-target species, such as crabs. We emulated aerial bait applications by positioning opened ADS cartridges on a simulated branch (45-cm wooden dowel) with the DNM hanging in the field of view (FOV) of a camera mounted atop a painter's pole, extended into the forest canopy and temporarily lashed to natural vegetation with bungee cords (Fig. 3A).

Ground presentation: As some ADS baits fail to tangle in the canopy or DNM may become unstuck from the cartridge and fall through to the forest floor, we sought to evaluate the fate of DNM on the ground. Additionally, recent evidence

Figure 3. Camera orientations for canopy and ground bait monitoring **A** infrared camera set-up mimicking aerial application of dead neonatal mouse (DNM) baits via the USDA Wildlife Services Aerial Delivery System (ADS) for landscape-scale brown treesnake control; the camera and bait are elevated into the forest canopy atop a telescoping painter's pole **B** ground bait monitoring set-up, with an infrared camera mounted directly over a large mouse (LM) bait on a tripod constructed from extruded metal tubing (conduit); the bait and a lightweight PVC background with circular size standards were lashed to a 0.9-kg lead diving weight to prevent small crabs from dragging the bait out of the camera's field of view.

indicates that ADS treatments might not adequately expose large brown treesnakes to baits; larger brown treesnakes on prey-depleted Guam are more prone to foraging on the ground, might be preferentially attracted to larger baits and might require greater doses of acetaminophen for effective removal (Rodda and Reed 2007; Nafus et al. 2020; Goetz et al. 2021; Siers et al. 2021). Moreover, the estimated take rates for large ground baits in a treated population on Guam is greater than for standard ADS baits (Nafus et al. 2022). For these reasons, USDA Wildlife Services has considered an alternative aerially delivered bait system comprising a slightly larger mouse (SM) placed in the same bait cartridge tube, but without the ribbon assembly, which would let the bait fall to the forest floor where larger snakes may be more effectively targeted (Siers et al. 2021). We also considered that even larger baits placed on the forest floor, potentially containing larger doses of acetaminophen, could more effectively target larger ground-foraging snakes, so we incorporated LM and LB into ground presentations. Ground baits were placed on small, thin PVC plastic platforms printed with 20-cm size standards and lashed to a 0.9-kg. lead diving weight to prevent small crabs from dragging the bait out of the field of view of the cameras. Cameras were mounted directly overhead on tripods fashioned from inexpensive extruded metal tubing (conduit; Fig. 3B). Brown treesnake head measurements taken from overhead images containing a size standard can be used to estimate snake size (Siers 2021). As both canopy and ground baits are not protected from being taken by non-target species, we did not treat these baits with acetaminophen tablets for this pilot evaluation.

Bait station presentations: Polyvinyl chloride (PVC) tube bait stations ('bait tubes') are intended to exclude non-target species that might interfere with baits, making them unavailable to brown treesnakes and to protect native species from unintentional exposure to acetaminophen intoxication. Standard operational baiting methods include placing a DNM treated with a tablet containing 80 mg of acetaminophen into a 5-cm diameter, 30-cm long PVC bait tube, with 6.35-mm bolts crossing the openings at the ends to further prevent ingress by non-targets. Bait tubes are usually suspended horizontally by two lengths of paracord from existing vegetation or structures, such as fence lines (Savarie et al. 2001; Clark et al. 2012; Lardner et al. 2013; Clark et al. 2018). Based on the average size of brown treesnakes recovered from Cocos Island prior to the testing of these tools (Barnhart et al. 2022), we elected to deploy larger baits (SM, LM, SB and LB) within our bait stations on Cocos Island. We evaluated standard 5 × 30-cm horizontal bait tubes (Fig. 4A), as well as alternative designs intended to more reliably exclude non-target species, such as crabs and Mariana monitors (e.g. Mathies et al. (2011)): longer 5 × 45-cm horizontal bait tubes (Fig. 4B); vertical 5-cm diameter × 30-cm long bait tubes capped at the top end (Fig. 4C); and capped vertical 10-cm diameter × 30-cm long bait tubes (Fig. 4D). Both horizontal bait tube designs included bolts across the openings, whereas vertical tubes did not to prevent use of the bolts by non-targets to assist climbing into the tubes.

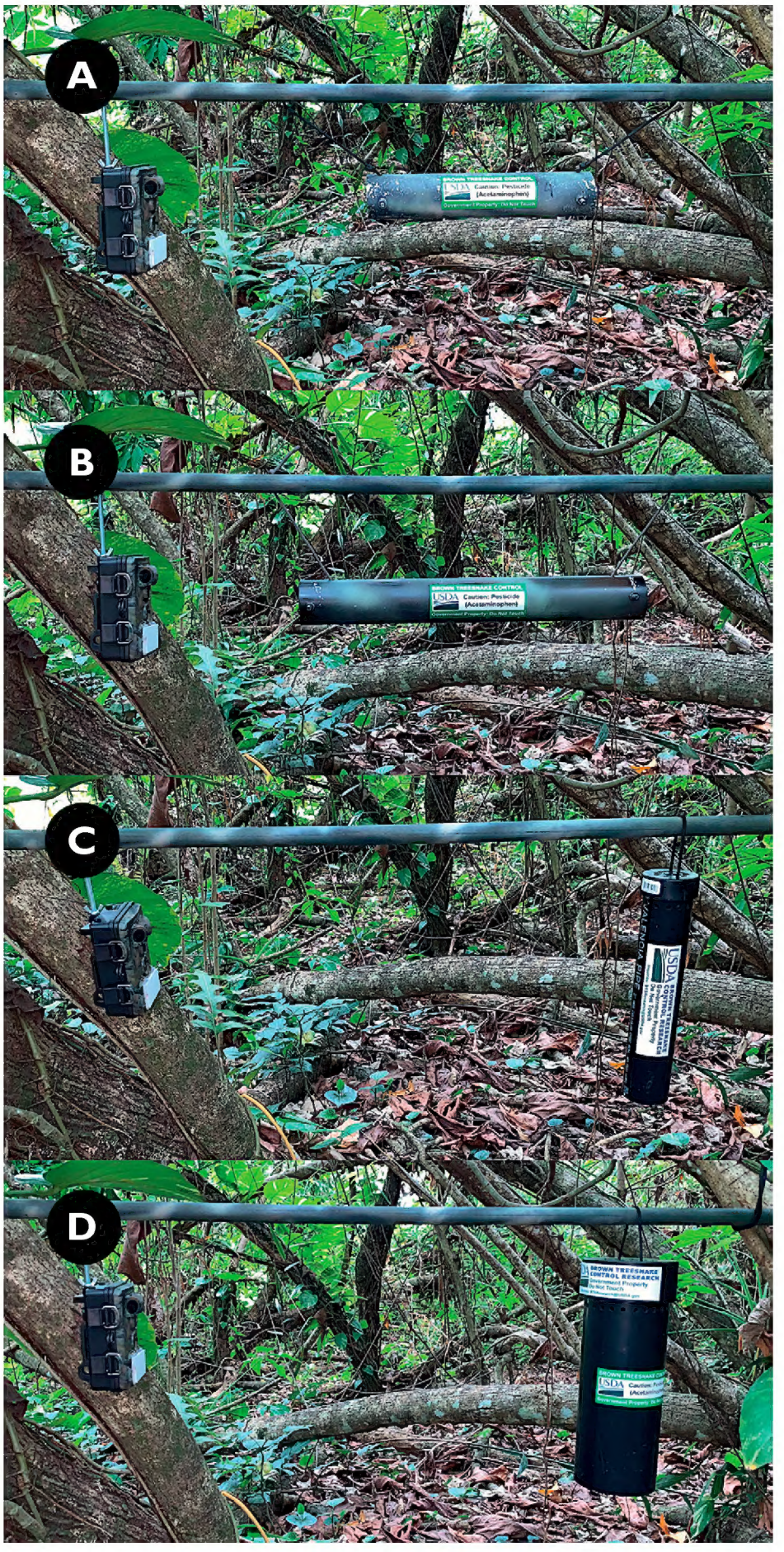

Figure 4. Camera orientations and bait station configurations for bait monitoring **A** standard 5-cm diameter × 30-cm long polyvinyl chloride (PVC) horizontal bait station suspended by nylon paracord from a wooden dowel armature with infrared camera positioned with the bait in the field of view; the two ends of the armature are temporarily lashed to natural vegetation with elastic cords **B** extended 5 × 45-cm horizontal bait tube **C** capped 5 × 30-cm vertical bait tube **D** capped 10 × 30-cm vertical bait tube. Baits in horizontal bait tubes were held in place by gravity, while baits were held in the caps of vertical bait tubes by spring clamps on one foot of the bait. As baits in vertical bait tubes were not visible to the camera, a length of biodegradable flagging was tied to one leg of the bait and pulled through a small hole in the side of the tube for ease of identifying when the bait was taken during camera image review.

We suspended all bait station types by paracord from a wooden dowel armature to which the trail camera was affixed, locking the bait in the FOV of the camera. We temporarily attached these armatures to existing vegetation by elastic cords, with minor vegetation pruning to ensure that leaves or branches did not obstruct the view of the bait. We placed baits in the centre of horizontal tubes where they were held in place by gravity and friction alone. Within vertical bait tubes, we attached baits within the caps clipping one foot with a small metal spring clamp, holding baits in place, but making them easily removed with a slight tug from snakes or non-targets. As cameras could not directly view baits in the vertical tubes, we tied a length of white biodegradable flagging tape to one leg of each bait and pulled the tape through a small hole in the side of the tube; when the bait was removed, the flag disappeared and the animal within the FOV of the camera at that time was attributed with the bait removal.

As bait stations offered some degree of protection from non-target interference, we treated baits in bait stations with tablets containing 80 mg of acetaminophen inserted into the body of the bait via the oral cavity, to remove any brown treesnakes that took baits.

We spaced bait placements at approximately 20-m intervals along existing paths and trails on Cocos Island (Fig. 1); entry into the forest was not authorised prior to a formal endangered species consultation process with the U.S. Fish and Wildlife Service. Paths were subdivided into nine, segments (transects). Each week we placed 36 bait monitoring stations along one transect, alternating each of three presentation types (12 stations each). We monitored each transect of 36 stations for one week, with the bait checked and replaced once mid-week with a fresh bait, for baiting intervals of 3 to 4 days. Beyond 3 to 4 days, baits are degraded through putrefaction and consumption by ants and fly larvae and are no longer considered viable for take by brown treesnakes. During Weeks 1–9 (12 December 2020–16 February 2021), we placed canopy, ground and standard 5 × 30-cm horizontal tubes (Figs 3A, B, 4A) in alternating positions along each transect, with bait types alternated as appropriate to the objectives of the presentation type. During Weeks 10–18 (18 February 2021–22 April 2021), we alternated 5 × 45-cm horizontal tubes and the two vertically orientated tube types (5 × 30 and 10 × 30 cm; Fig. 4B–D), along with alternating bait types. At bait checks, if a bait appeared to have been taken, we reviewed camera images to identify the time of bait removal and the species taking the bait.

This portion of the study was performed during Guam's cooler, drier months. Average daily temperatures for Guam ranged from highs of 30.4 °C (standard deviation = 0.903 °C) to lows of 24.7 °C (SD = 1.03 °C) and rainfall averaged 2.16 mm/day (SD = 5.3 mm/day, max = 48 mm/day), based on National Oceanic and Atmospheric Administration data (www.weather.gov).

Live trapping

After years of experimentation with multiple live trap designs, a modified crayfish or minnow trap was adopted as the standard brown treesnake live trap used on Guam. The original trap is a two-piece dual-funnel design of galvanised wire mesh with the entrances modified with a PVC ring holding a one-way wire mesh flap that allows ac-

cess to the trap body, but blocks escape by snakes (Fig. 5, left). Rodda et al. (1999b) showed this trap to be the most effective trap known for any snake at the time. Snakes are lured into the traps by a live mouse in a protected wire mesh chamber held within the trap body. This two-piece design was later adapted for operational purposes by creating a single-piece body of more durable stainless steel, accessed by removing one of the funnel ends and incorporating the mouse chamber into the trap body so that the mouse can be serviced without opening the trap; this version of the trap is referred to as the USDA Wildlife Services "WS Standard" (Fig. 5, centre; Vice et al. (2005)). In both trap types, mice are provisioned with a custom-made block of commercial seed and pellet mix embedded in a paraffin wax matrix which prevents exposure to the elements until the mouse chews through the wax (Fig. 5, right). A piece of fresh potato provides the necessary water.

The use of live mouse lures is less than desirable due to maintenance expense and perceptions regarding animal welfare; however, despite extensive efforts, no trap lure has been found to be nearly as effective and practical as a live mouse (Chiszar 1990; Shivik and Clark 1997; Shivik 1998, 1999; Lindberg et al. 2000). Prior to verification of brown treesnake presence on the Island, Guam's Division of Aquatic and Wildlife Resources (GDAWR) performed surveillance trapping using dead mouse and rat lures due to concerns about escaped live mice establishing a population on the Island (D. Vice, GDAWR, written communication, 2023) but no snakes were ever captured in these traps. Prior to this study, there were no reported head-to-head tests of live versus dead mouse lures in brown treesnake traps.

To evaluate differences in efficacy and durability between trap types and capture success between live and dead mouse lures, we alternated 99 one-piece WS Standard and 99 original two-piece traps approximately every 20 m along the same existing trails as the previous baiting trials (Fig. 1). We alternated live and dead mouse lures between

Figure 5. Two types of traps used. Left: Galvanised wire mesh two-piece trap with separate live mouse lure chamber within the trap body. Centre: Stainless steel one-piece Wildlife Services Standard trap with integrated live mouse lure chamber. Right: Integrated lure chamber in one-piece trap showing live mouse, feed block of pellets and seeds immersed in paraffin wax and piece of fresh potato to provide moisture; mice in both trap types are provisioned in this manner.

every pair of two trap types (repeating the order of one-piece/live, two-piece/live, one-piece/dead, two-piece/dead etc.) for a total of 100 traps with live mouse lures and 98 with dead mice. Following the typical use patterns of these two trap types, we hung one-piece traps on nylon paracord and two-piece traps on metal tie wire, at about waist to chest height on existing vegetation. We checked traps twice weekly (every 3 or 4 days) for 55 nights, provisioning live mouse lures and replacing dead mouse lures with fresh dead mice. We recorded brown treesnake captures, non-target captures and trap damage caused by non-target species. We also recorded traps as non-functional when missing lures, with funnel flaps stuck open or closed, with large holes due to crab damage or with other defects making them unlikely to capture or prevent escape by snakes. As traps were confirmed to be functional at the beginning of each trap-checking interval, we assumed traps became non-functional approximately mid-interval, on average, so reduced our tally of effective trap nights by one-half of the checking interval per non-functioning trap, similar to methods of Nelson and Clark (1973). Trapping results are reported as captures per unit effort (CPUE) or snake captures per night per trap.

We monitored a subset of 20 traps via infrared game cameras (Hyperfire 2, Reconyx, Holmen, Wisconsin). We distributed 10 cameras evenly along a rock retaining wall and another 10 along a transect through a bird roosting area. We positioned half of these cameras on traps with live mouse lures and the other half on traps with dead mice. We recorded time-lapse images (one photo every 60 seconds) between 1800 and 0600 h to observe for brown treesnakes investigating traps, but failing to enter, as has been documented on mainland Guam (Yackel Adams et al. 2019; Amburgey et al. 2021).

We performed trapping from 17 June to 12 August, 2021, earlier months of Guam's warmer, rainier season. Guam daytime highs averaged 31.4 °C (SD = 1.04) with night-time lows of 25.6 °C (SD = 0.969) and rainfall of 9.22 mm/day (SD = 13.5mm, max = 71.9mm) (www.weather.gov). We measured snout-vent length (SVL, mm) of trapped snakes by gently stretching them along a flexible tape and measured weight using handheld spring scales with maximum ranges from 10 g (0.1 g precision) to 1000 g (10 g precision) (Pesola, Schindellegi, Switzerland). We determined sex by probing for inverted hemipenes with steel sexing probes (Reed and Tucker 2012).

Visual detection during rapid response

Throughout the evaluation of control tools, USGS conducted nocturnal visual searches and hand-removal of brown treesnakes (December 2020 through July 2021). Methods followed those applied on Guam in which individuals surveyed transects after dusk using powerful headlamps (Wilma, Lupine Lighting System, Lebanon, PA, USA) walking a slow searcher pace, such that each transect (~ 400 m) lasted approximately 1 hour. During snake searches, observations of potential prey items (lizards, birds and bats) were recorded. Visual survey data are available for download (U.S. Geological Survey 2023). These searches were also limited to the cart paths and trails depicted in Fig. 1. We recorded SVL, weight and sex for captured snakes as above.

Statistical methods

All summary statistics, statistical tests and graphing were performed in the R environment for statistical computing, Version 4.2.2 (R Core Team 2021). We evaluated the likelihood that an unobserved bait take due to camera malfunction could have been taken by a snake by describing the 95% confidence interval of brown treesnake bait takes given the successfully observed baits (binom.confint, method = "exact"). We evaluated differences in duration of bait availability amongst presentation types with Cox proportional hazard survival models function coxph), with trials ending when the bait was taken by a non-target or when the three to four days monitoring period was over. Differences in trap capture rates amongst trap types and trap lure types were calculated using Fisher's exact tests with 95% confidence intervals (fisher.test).

Ethics statement

This study was carried out in compliance with relevant laws and guidelines. All animal use was approved by the USDA National Wildlife Research Center Institutional Animal Care and Use Committee under protocols QA-3106 and QA-3340 and USGS Institutional Animal Care and Use Committee protocol 2021-02. Compliance with the Endangered Species Act was ensured through informal consultation with the U. S. Fish and Wildlife Service (01EPIF00-2021-I-0087 and 01EPIF00-2021-I-0087-R001).

Results

Acetaminophen baiting

After eliminating incomplete trials (camera failure etc.), we successfully monitored a total of 1,250 baits between December 2020 and April 2021. During these trials, we observed no baits being investigated or taken by brown treesnakes. As there were no bait takes by brown treesnakes, we could not make comparisons of bait take rates amongst bait types or presentation types. Of the 701 baits that were taken, we could not identify the species in 30 (4.3%) of the cases. The 95% binomial confidence interval for brown treesnake takes for the 671 baits for which a species ID was confirmed is 0–0.548%; if this rate were applied to the 30 unknown takes, the upper confidence limit for brown treesnake bait takes would be 0.164 baits; thus, we consider it highly unlikely that any of the unknown animals taking these 30 baits was a brown treesnake.

A high overall proportion of the baits (56.1%) were taken by non-target species (Fig. 6), primarily by coconut crabs and Mariana monitors. Canopy baits were removed by coconut crabs (11.5%), Mariana monitors (12%) and insects (11.5%, mostly ants and fly larvae), while 20.7% fell from the simulated bait cartridge due to putrefaction or consumption by insects. One bait was removed from the bait cartridge by a large gecko (*Gehyra oceanica*). Of the DNM baits in the canopy, 43.8% remained available (i.e. were not taken by non-targets), but were not observed being investigated or taken by brown

treesnakes. All but three baits placed directly on the ground were taken by non-targets, mostly coconut crabs and Mariana monitors, with some take by hermit crabs (*Coenobita* spp.) and land crabs (likely *Cardisoma carnifex* or *Discoplax* spp.). One DNM ground bait was taken by a Pacific reef heron (*Egretta sacra*) and another by a Guam rail. Of baits offered in the standard 5 × 30-cm horizontal tubes, 66.3% were taken by Mariana monitors and coconut crabs. The other bait station designs successfully repelled almost all coconut crabs; Mariana monitors continued to be the primary challenge for all bait station types, but the 5 × 45-cm horizontal tube reduced monitor takes to only 15.8% (Fig. 6).

Coconut crabs and Mariana monitors were by far the most common consumers of baits. Plotting the recorded time of bait takes by coconut crabs and Mariana monitors (Fig. 7) reflected clear patterns of nocturnal activity for coconut crabs and diurnal activity for Mariana monitors, with bimodal peaks of monitor activity in early morning and late afternoon.

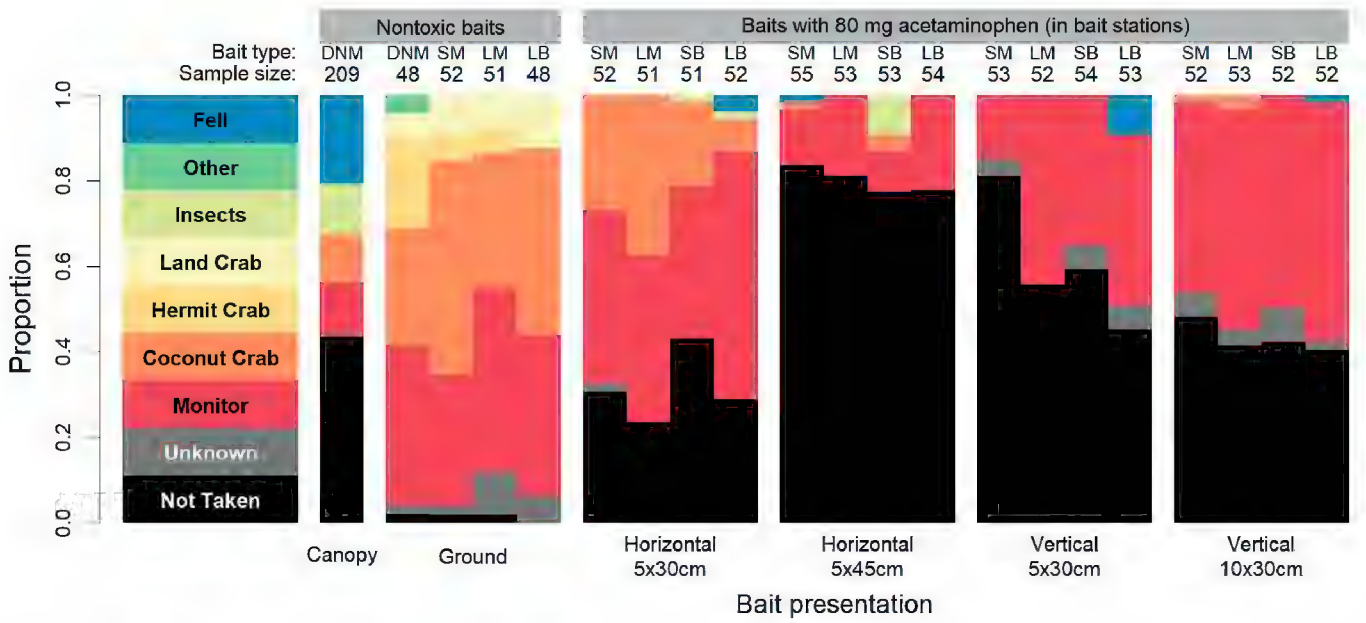
Nontoxic baits
Baits with 80 mg acetaminophen (in bait stations)
Bait type: DNM DNM SM LM LB SM LM SB LB SM LM SB LB SM LM SB LB SM LM SB LB
Sample size: 209 48 52 51 48 52 51 51 52 55 53 53 54 53 52 54 53 52 53 52 52
Fell
Other
Insects
Land Crab
Hermit Crab
Coconut Crab
Monitor
Unknown
Not Taken
Proportion
0.0 0.2 0.4 0.6 0.8 1.0
Canopy
Ground
Horizontal 5x30cm
Horizontal 5x45cm
Vertical 5x30cm
Vertical 10x30cm
Bait presentation

Figure 6. Fates of carrion baits applied on Cocos Island. No brown treesnakes were observed taking any baits. DNM = dead neonatal mouse (4–6 g); SM = small mouse (10–14 g); LM = large mouse (25–35 g); SB = small birds (10–14 g quail chick); LB = large bird (25–35 g chicken chick). Sample size is the number of baits successfully monitored after eliminating incomplete trials.

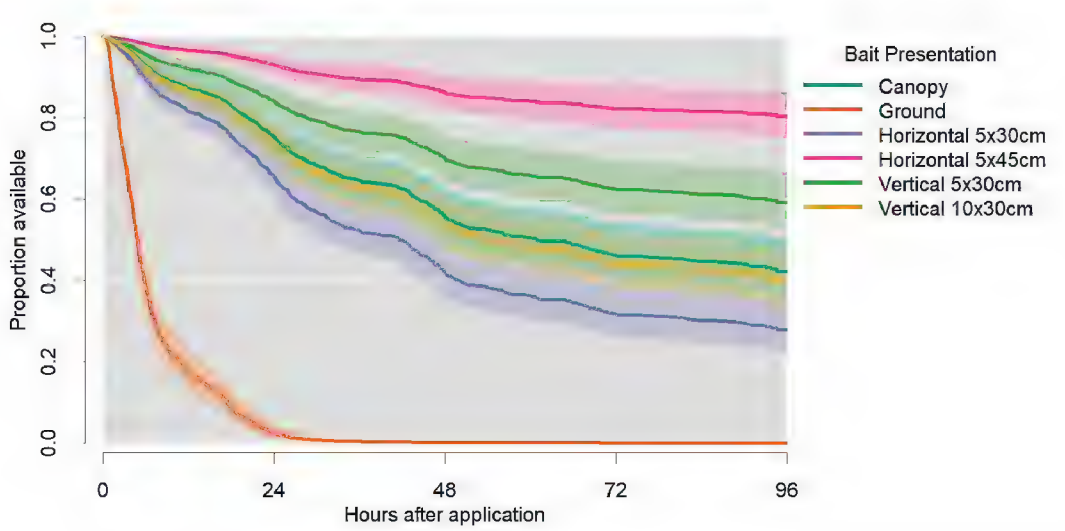

Figure 7. Times of bait removal by the primary non-target consumers on Cocos Island. Most baits were removed by coconut crabs (*Birgus latro*) and Mariana monitors (*Varanus tsukamotoi*). Light grey strips indicate changes in sunrise and sunset over the study period.

We recorded the duration of bait availability before being taken by non-targets or removed at the end of the trial and subjected these data to survival analysis (Fig. 8). Non-targets removed almost all ground baits within 24 hours. The horizontal 5 × 45-cm bait tube clearly outperformed all other presentation types, with 80% of the baits remaining at the end of the observation period.

Summing all the time that baits were available to brown treesnakes before being taken by non-targets, we recorded a total of 2,427 "bait days" with no takes by brown treesnakes. This amounts to an overall daily estimated brown treesnake bait take rate of 0.000 per 100 bait days with an upper 95% binomial confidence interval of 0.151 baits per 100 bait days.

Trapping

We operated 198 traps (99 one-piece, 99 two-piece) with mouse lures (100 live, 98 dead) for 55 nights, for a total of 10,890 trap nights (Table 1) between and June and

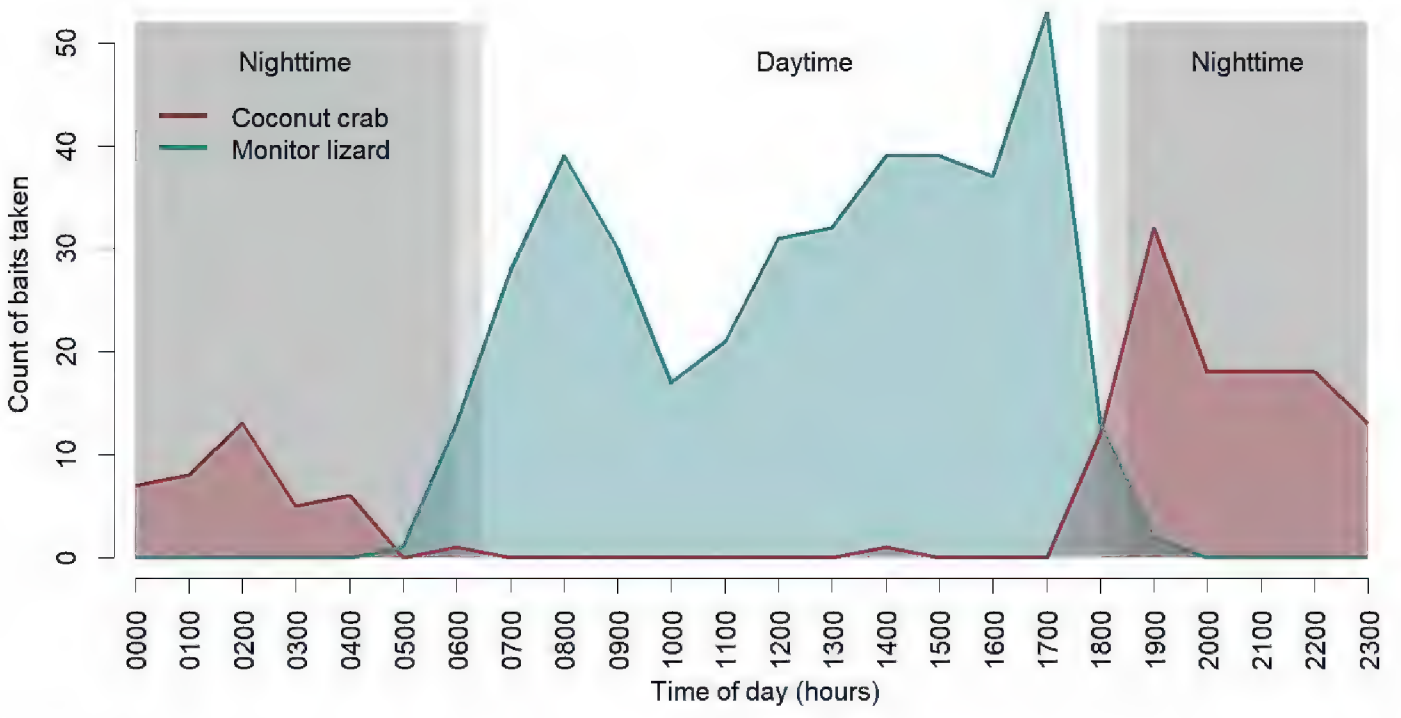

Figure 8. Persistence of all baits offered in various presentation types. Curves depict reduction in proportion of baits available over time as non-targets remove them. Baits typically decline in viability through putrefaction and consumption by insects after 48 to 96 hours. Shaded areas represent 95% confidence intervals.

Table 1. Trapping effort (trap nights) by trap type and lure type. Values reflect overall effort and effort adjusted for non-functioning traps (e.g. lure missing, entrance flaps stuck open or closed, holes due to crab damage). Traps were functional at the previous check, so non-functional traps were presumed to be functional for one-half of the check interval, on average.

Trap type	Overall effort (trap nights)			Adjusted for non-functioning traps		
	Live mouse	Dead mouse	Total	Live mouse	Dead mouse	Total
One-piece	2,750	2,695	5,445	2,682.5	2,620.0	5,302.5
Two-piece	2,750	2,695	5,445	2,663.0	2,588.0	5,251.0
TOTAL	5,500	5,390	10,890	5,345.5	5,208.0	10,553.5

August of 2021. After adjusting for non-functioning traps, we achieved an effort of 10,553.5 effective trap nights.

During this effort, we captured only one brown treesnake: a 1,249-mm SVL male weighing 360 g (Fig. 9). The snake was captured in a two-piece galvanised trap with a live mouse lure. One capture in 10,553 trap nights yields a combined CPUE of 9.47^{e-5} or 0.00947 captures per 100 trap nights. Considering CPUE only for traps with live mouse lures increased CPUE to 0.0187 captures per 100 trap nights. The 95% binomial confidence interval for trap success (probability of each trap capturing at least one snake on a given night) with a live mouse lure is 0.000473 to 0.0528 trap successes per 100 trap nights.

Non-target lizards and crabs were commonly found in brown treesnake traps (Table 2). As with acetaminophen baiting, coconut crabs and Mariana monitors were the most significant non-targets, being large and powerful and capable of damaging traps. Smaller lizards were more common in traps with dead mouse lures, likely drawn by flies and other insects feeding on the carrion lure. Crabs, including coconut crabs, were more often found in the one-piece WS standard traps, possibly because one-piece traps were hung with nylon paracord, per WS standard operations, while two-piece traps were hung by metal tie-wire; it is conceivable that metal wire provides less purchase for crabs attempting to access traps. Crabs were more prevalent in traps with live mouse lures, probably attracted by feed waste and faeces generated by the mouse.

Figure 9. The only brown treesnake captured in over 10,500 trap nights on Cocos Island. This was a 1,249 mm snout-vent length, 360 g, male. This trap contained a live mouse in a protected chamber as the lure.

Table 2. Non-target captures in brown treesnake traps. Results are tabulated by trap type (one-pieces stainless steel versus two-piece galvanised) and lure type (live mouse or dead mouse). Counts are per trap observation; multiple individuals in the trap at the same time are counted as only one observation.

Common name	Latin name	One-piece Live	Two-piece Live	One-piece Dead	Two-piece Dead	Total
Lizards						
Green anole	*Anolis carolinensis*	1	0	2	3	6
Blue-tailed skink	*Emoia caeruleocauda*	0	0	1	0	1
Oceanic gecko	*Gehyra oceanica*	0	0	2	0	2
Other geckos	Gekkonidae	1	1	1	1	4
Mariana monitor	*Varanus tsukamotoi*	8	11	14	5	38
Crabs						
Hermit crabs	*Coenobita* spp.	183	24	14	1	222
Coconut crab	*Birgus latro*	57	9	22	17	105
Totals		250	45	56	27	378

Stainless steel one-piece traps were non-functional for 5.2% of trap nights, while galvanised two-piece traps were non-functional for 7.1% of nights ($P < 0.001$). Live mouse lure traps were non-functional 5.6% of trap nights and dead mouse lure traps were non-functional 6.8% of nights ($P = 0.015$). Stainless steel one-piece traps required 21 field repairs for a total of 2.83 hours of labour, while galvanised two-piece traps required 82 repairs totalling 12.4 hours of field labour. Only one trap, a two-piece galvanised trap, was removed for workshop repairs. At the end of the trapping effort, repair and cleaning requirements were recorded by trap type (Table 3). The one-piece stainless steel traps were more durable to crab damage and required less labour to fix, primarily straightening deformations of unbroken wire mesh, while all damaged two-piece galvanised wire traps required more serious repairs, such as hole patches. No traps of either type were damaged beyond repair. Although galvanised wire traps are likely more prone to corrosion than stainless steel over prolonged use in the near-marine environment, there was little noticeable corrosion over the course of this study. The one-piece traps required more time to clean due to the lure chambers being integrated into the trap body.

Table 3. Repair and cleaning requirements by trap type. Minor repairs included straightening wire deformations from coconut crab damage, while major repairs required patching of holes in the mesh from crab damage.

Trap type	No repair (n)	Minor repair (n)	Major repair (n)	Repair labour (hr)	Cleaning labour (hr)
One-piece stainless steel	28	47	24	13	20
Two-piece galvanised wire	31.5*	0	67.5	27	7
Totals	59.5*	47	31.5	40	27

* The two-piece traps were recorded by interchangeable trap halves (two halves = one trap), hence the 0.5-trap increments.

During 1,100 trap nights monitored by infrared cameras (20 cameras, 647,733 total photos), we recorded only two trap encounters by brown treesnakes, of 2 and 8 minutes in duration (Fig. 10). In neither of these cases did the snake successfully enter the trap. Both recorded encounters were of a similarly-sized snake on the same trap with a live mouse lure 10 nights apart; we believe it reasonable to consider these to be two observations of the same snake.

Visual detection during rapid response

Throughout the time period of our baiting and trapping efforts (December 2020 to July 2021), USGS personnel performed 163.3 km of linear search effort over 376 hours and sighted 31 snakes, three of which escaped capture, for a visual detection rate of 0.188 snakes per km and 0.083 per hour of search. Prey sighting rates were high, with an average lizard sighting rate of 37.8/km (including 10 species) and 32.8 birds/km (8 species). Specifically for notable species, sighting rates were 15.5 green anoles, 11.3 oceanic geckos, 22.3 black noddies and 8.1 white terns per km of searching (U.S. Geological Survey 2023). The mean SVL of snakes captured and removed was 1073 ± 295 (range: 650, 1622) and mean weight was 256 ± 195 g. The demography of the population encountered was biased towards snakes typically attracted to endothermic prey (60% of 28 captures > 900 mm SVL).

Figure 10. A large brown treesnake at a two-piece trap with a live mouse lure recorded via time-lapse infrared photograph. The snake probed the body of the trap for 8 minutes, then left without returning that night. A snake of a similar size (likely the same snake) attempted to enter the same trap for 2 minutes 10 days later.

Discussion

The results of this study are clear: two of the primary tools for brown treesnake removal on Guam will not be effective for brown treesnake eradication on Cocos Island. Brown treesnake detection rates, based on visual CPUE, are apparently lower on Cocos Island (0.188 snakes/km) than most other detection efforts on Guam. Within a long-term 5-ha geographically enclosed population representative of disturbed limestone forest and secondary forest on Guam, Nafus et al. (2023) recorded 0.758 brown treesnakes per km of transect searched. In a 55-ha snake enclosure surrounding degraded limestone forest in northern Guam, Boback et al. (2020) documented a CPUE of 0.906 brown treesnakes per searcher hour, compared to 0.083 on Cocos Island. Following aerial baiting at this same site (Dorr et al. 2016; Siers et al. 2018), the CPUE dropped to 0.049 per hour, lower than the Cocos Island CPUE. With all of the caveats that come with using CPUE as an index of relative abundance (e.g. detectability differences amongst different habitat types), these data demonstrate that visual detection rates on Cocos Island are lower than unmanipulated habitat on Guam (24% compared to Nafus et al. (2023) per km and 9.2% compared to Boback et al. (2020) per hour before aerial suppression), but nearly twice as high as within an aerially-suppressed study plot (Boback et al. 2020). Nonetheless, despite 40% lower visual contact rates than on Cocos Island, the suppressed population on Guam continued to take non-toxic dead mouse baits at rates averaging approximately 20% (Siers et al. 2018b), while the Cocos Island bait take rate was 0%.

Live trapping with mouse lures prior to snake suppression on Guam yielded a capture rate of 0.3 snakes per 100 trap days (Nafus et al. 2018). These differences in snake detection rates by location indicate that greater bait or trap captures on Cocos Island would be expected given the level of effort we applied to each tool. Carrion bait take rates on Guam in areas without active brown treesnake control tend to range from approximately 30% to nearly 100% (Savarie et al. 2001; Clark and Savarie 2012; Siers et al. 2018b, 2019b, 2020a), while we failed to observe a single bait take within 2,427 bait monitoring days (upper 95% confidence interval of 0.151%). Trapping captures per 100 trap nights on Guam are commonly higher in areas where they are not being operationally suppressed, (4–9; Nafus et al. (2018)) and ranged as high as 25 to 60 in the 1990s (Rodda et al. 1999b). In areas on Guam in which brown treesnakes have been suppressed to 0.16 snake/ha (as estimated from forest interior visual survey CPUE), trapping CPUE was maintained at the rate of 0.3 captures per 100 trap nights (Nafus et al. 2018; Boback et al. 2020). When using live mouse lures on Cocos Island, we achieved only 0.0187 captures per 100 trap nights which is substantially lower than the anticipated levels based on Guam efforts (Guam CPUE 213 to 481 times higher than Cocos Island when compared to Nafus et al. (2018) results).

Our failure to attract brown treesnakes to baits and traps is most likely due to the extraordinary abundance of preferred live prey on Cocos Island, particularly large geckos, birds and their eggs, compared to the relatively prey-depauperate nature of Guam's forests resulting from prolonged brown treesnake predation (Fritts and Rodda

1998; Wiles et al. 2003; Siers 2015). Cocos Island is populated by abundant lizards, many of which have been extirpated from parts or all of Guam by brown treesnake predation, such as federally and locally endangered Mariana skinks, locally endangered littoral skinks (*Emoia atrocostata*), fragile Micronesian geckos (*Perochirus ateles*) and Pacific snake-eyed skinks (*Cryptoblepharus poecilopleurus*), as well as mutilating geckos (*Gehyra mutilata*), oceanic geckos (*G. oceanica*) and green anoles (*Anolis carolinensis*). Small brown treesnakes, in particular, appear to be specialists on small lizards, which are an almost exclusive prey item in stomach contents (Savidge 1988; Siers 2015). They also exhibit strong preference during laboratory feeding trials (Lardner et al. 2009) and present a venom composition that is more effective for ectotherms as juveniles (Mackessy et al. 2006). Our green anole sighting rates were relatively high (15.5/km), but close to estimates from the snake-free island of Saipan (14.9/km; Lardner et al. (2019a)), while observations of this species in brown treesnake stomach contents from mainland Guam are extremely low in forest habitats, from where they have been essentially extirpated by brown treesnake predation (Rodda and Fritts 1992; Siers 2015). Relatively large oceanic geckos, which are roughly equivalent in mass to a small mouse, may additionally offer a rewarding prey item that reduces the efficacy of bait- and lure-based control tools on Cocos Island. We commonly observed oceanic geckos on Cocos Island (11.3/km), while they are no longer documented in brown treesnake stomach contents on mainland Guam (Siers 2015), having been essentially extirpated by brown treesnake predation (Rodda and Fritts 1992). Nafus et al. (2023) recorded no observations of green anoles or oceanic geckos and their total lizard sighting rates were 6.0/km (4 species) compared to 37.8/km (10 species) on Cocos Island, indicating substantially greater lizard prey availability. Unchecked brown treesnake predation and population growth could put all small lizard species at risk of almost certain local extinction on Cocos Island (Rodda and Fritts 1992; Rodda et al. 1997; Fritts and Rodda 1998; USFWS 2019).

Of all the ecological damage that have occurred since their introduction to Guam, the pervasive impacts of brown treesnake predation on birds have been the most profound (Savidge 1987; Wiles et al. 2003; Pollock et al. 2019; Klug et al. 2021b). Our Cocos Island bird sighting rate of 32.8/km and 11.3/hour is high, given the well-documented collapse and functional extinction of the forest bird avifauna on mainland Guam (Savidge 1987; Wiles et al. 2003). Any experienced brown treesnake searcher can attest that bird sightings in forest habitats on mainland Guam are quite rare, earning Guam its reputation for "silent forests" and the cascading ecological effects of bird loss (Savidge 1987; Rodda et al. 1997; Rogers 2011, 2020). Nafus et al. (2023) documented only four bird sightings of indeterminate species in 816.2 km of transect searching in the northern Guam 5-ha enclosure (0.005 birds/km). It is unclear how severely brown treesnake predation on Cocos Island has affected the abundance of bird and lizard prey species, but prey resources clearly remain much more abundant on Cocos Island.

Brown treesnakes on Guam that forage in areas of increased prey availability, including birds, such as urban areas and swiftlet caves, tend to be in better body con-

dition (Siers 2015; Siers et al. 2017b; Yackel Adams et al. 2019; Klug et al. 2021b), a characteristic that is evident in the extremely heavy snakes that have been found during visual surveys on Cocos Island. The mean weight of snakes reported in other contemporary studies on Guam (Siers et al. 2017b) suggests that the average weight of snakes removed from Cocos Island during the period of this study is much greater. There is also emerging evidence that brown treesnakes conditioned to feeding on live birds exhibit less attraction to rodent-based baits and lures (Nafus et al. 2021). During brown treesnake removal from Cocos Island, encounters with seabirds, Guam rails and Micronesian starlings (*Aplonis opaca*) were not uncommon (U.S. Geological Survey 2023), supporting the impression that avian prey currently remain abundant on Cocos Island relative to Guam. For these reasons, it is apparent that, although brown treesnakes on Guam will readily consume carrion, live lures are far more effective than any dead animal baits or other inanimate lures (Shivik et al. 2000; Savarie and Clark 2006; Kimball et al. 2016) and that the availability of abundant preferred prey (birds) on Cocos Island diminishes the attraction to carrion baits.

These findings demonstrate that higher prey availability negatively affects brown treesnake detection and capture rates. On Guam, temporary experimental suppression of rodent prey abundance was demonstrated to increase trap capture rates (Gragg et al. 2007) and increasing movement distances of brown treesnakes (Christy et al. 2017). Free-ranging brown treesnakes that have recently taken large meals have been experimentally demonstrated to significantly reduce movement for 5 to 7 days, with an associated reduction in the ability to visually detect or trap snakes during this time (Siers et al. 2018a). Foraging for carrion may also be a futile strategy for brown treesnakes on Cocos Island where coconut crabs and Mariana monitors rapidly remove all carrion from the ground (Figs 7–9). Moreover, prior studies have indicated that brown treesnake attraction to carrion and especially mouse carrion, may decrease as snakes increase in size (Shivik and Clark 1999; Nafus et al. 2021), while large snakes may be the most important demographic to remove from the perspective of both avian conservation and eradication potential (Savidge 1988; Yackel Adams et al. 2019; Nafus et al. 2022).

Both baiting and trapping appear to be relatively safe for Cocos Island wildlife. In only two instances did a native bird (a Pacific reef heron and a Guam rail) take a bait (both DNM) from the ground. Although acetaminophen may also be toxic to birds, they are not known to have the same genetic basis for sensitivity to acetaminophen toxicosis as snakes (van den Hurk and Kerkkamp 2019) and crows in cage trials picked around acetaminophen tablets rather than ingesting them, with no signs of toxicosis (Avery et al. 2004). Clearly, crabs and Mariana monitors quickly cleanse the forest floor of any carrion baits containing acetaminophen. Crabs tend to eat around acetaminophen tablets when consuming carrion baits and show no signs of toxicosis (Johnston et al. 2002). On the other hand, Mariana monitors were the most problematic scavengers of baits on the ground and in bait stations and other monitor species are susceptible to acetaminophen toxicosis (Mauldin and Savarie 2010). Although recent evidence indicates that Mariana monitors are native to the Mariana Islands (Weijola et al. 2020), Mariana monitors on Cocos Island are being actively depredated

by GDAWR for the protection of endangered Guam rails and their nests. It is likely that several small Mariana monitors succumbed to acetaminophen toxicosis and would continue to do so if acetaminophen were used as part of a brown treesnake eradication programme on Cocos Island. Small Mariana monitors were also frequently caught live in traps; these could be released unharmed, but GDAWR requested that trapped Mariana monitors be removed and euthanised rather than released, in furtherance of their Guam rail protection efforts. Some small coconut crabs and hermit crabs expired in brown treesnake traps, likely due to dehydration, although the numbers would not be expected to have population-level impacts. Factors such as these need to be considered when assessing the potential environmental impacts of baiting or trapping for invasive snakes, although ineffectiveness in our case could make these issues moot.

The practical information on baiting and trapping is of little avail when brown treesnake removal by these techniques is almost completely ineffectual in the context of abundant alternative prey availability. Initial eradication discussions for Cocos Island included a notional plan of a 20 × 20-m grid of bait stations and a 40 × 40-m grid of traps. At this density, we might have arrayed as many as 825 bait stations and 206 traps with live mouse lures across the entire 33 ha of the Island for the duration of an eradication attempt that is expected to last at least 5 to 10 years (based on ad hoc population estimates and demographic projections; USDA Wildlife Services (2021a)). The pilot studies we report here have forestalled what might have been very costly investments in baiting and trapping with little or no payoff. Financial estimates for the costs of an island-wide baiting and/or trapping effort are beyond the scope of this article, complicated and inflated by considerations, such as boat travel, transect establishment etc., although these issues also affect visual search and removal efforts.

Instead, available funding is being programmed for visual searching and manual removal of snakes, the only tactic that has thus far been effective on Cocos Island. Although night-time visual searching can be logistically challenging, disruptive to work schedules and tedious, it is also the tool that is considered to be the least biased with respect to snake sizes, putting all brown treesnake size classes at risk of detection (Rodda et al. 2007; Christy et al. 2010; Yackel Adams et al. 2018; Lardner et al. 2019b). To date, there have been no documented successful invasive snake eradications beyond a temporary 1-ha experimental exclusion plot (Campbell et al. 2012); however, with judicious and sustained application of the right techniques, the small, isolated island of Cocos Island could potentially be the location of the first successful island-wide eradication.

Further work would be beneficial to validate whether live bird lures would be more effective than mice and carrion on Cocos Island. Field and laboratory experiments have demonstrated that traps with a live bird as the lure show increased capture rates of large, well-conditioned snakes, as well as longer trap investigation times overall compared to those with mouse lures (Yackel Adams et al. 2019; Klug et al. 2021a; Nafus et al. 2021). Additionally, a pattern of feeding success on birds may reduce a brown treesnake's interest in rodents and this may be particularly true on an island where rodents were eradicated in 2009. Verification of the disinterest of Cocos Island snakes to all potential attractant-based lures would be an important next step.

In the event of future invasions, prospects for complete removal of brown treesnakes from larger, prey-rich islands with difficult-to-access terrain would be challenging, particularly when our results indicate that application of the newly developed landscape-scale aerial baiting technology would be ineffective (Siers et al. 2020b). Work to differentiate between the context dependency of control tool attraction, based on total prey availability or species compositions of prey, can also be informative in amending current interdiction programmes or developing emergency response protocols if an incipient population of brown treesnakes is located on another island.

Conclusions

Our results indicate that standard invasive brown treesnake control tools, acetaminophen baiting and trapping with mouse lures, are seemingly not effective enough to warrant significant investment of limited project resources where preferred alternative prey are abundant. These results have profound ramifications for the potential of rapid removal and eradication of incipient brown treesnake populations on any other islands at risk of invasion, such as the Hawaiian Islands, the Northern Mariana Islands and throughout Micronesia and the rest of the Pacific where snake-free islands are rich in diversity and density of potential prey (e.g. Lardner et al. (2019a), Table 1). This work underscores the benefits of a continued emphasis on interdiction – prevention of accidental translocation through strong pre- and post-border inspections and reduction of potential stowaways in high-risk areas on Guam – over reliance on early detection and rapid response to resolve any new brown treesnake invasions that might occur. These results are also important for consideration of prevention, early detection, rapid response, suppression and/or eradication of other invasive snakes on islands or elsewhere. Similar issues are likely to be faced during any invasive snake removal programme, particularly where abundant alternative prey is available.

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References

Aguon CF, Campbell EW III, Morton JM (2002) Efficacy of electrical barriers used to protect Mariana crow nests. Wildlife Society Bulletin 30(3): 703–708. https://doi.org/10.7591/9781501737688-049

Amburgey SM, Yackel Adams AA, Gardner B, Hostetter NJ, Siers SR, McClintock BT, Converse SJ (2021) Evaluation of camera trap-based abundance estimators for unmarked populations. Ecological Applications 31(7): e02410. https://doi.org/10.1002/eap.2410

Avery ML, Tillman EA, Savarie P (2004) Responses of captive fish crows (*Corvus ossifragus*) to acetaminophen baits and bait stations for brown tree snake (*Boiga irregularis*) control on Guam. Bird Behaviour 16(1): 1–6.

Barnhart PD, Quiogue Z, Frasch ER, Vice D, Hopkins CB, Yackel Adams AA, Reed RN, Nafus MG (2022) Boiga irregularis (Brown Treesnake). Herpetological Review 53(3): 444–445.

Boback SM, Nafus MG, Yackel Adams AA, Reed RN (2020) Use of visual surveys and radiotelemetry reveals sources of detection bias for a cryptic snake at low densities. Ecosphere 11(1): e03000. https://doi.org/10.1002/ecs2.3000

BTSTWG (2015) Brown Treesnake strategic plan. Brown Treesnake Technical Working Group. November 2015, Agana, Guam, 86 pp.

Bushar LM, Reynolds RG, Tucker S, Pace LC, Lutterschmidt WI, Odum RA, Reinert HK (2015) Genetic characterization of an invasive *Boa constrictor* population on the Caribbean island of Aruba. Journal of Herpetology 49(4): 602–610. https://doi.org/10.1670/14-059

Campbell EW III, Yackel Adams AA, Converse SJ, Fritts TH, Rodda GH (2012) Do predators control prey species abundance? An experimental test with brown treesnakes on Guam. Ecology 93(5): 1194–1203. https://doi.org/10.1890/11-1359.1

Capinha C, Seebens H, Cassey P, García-Díaz P, Lenzner B, Mang T, Moser D, Pyšek P, Rödder D, Scalera R, Winter M, Dullinger S, Essl F (2017) Diversity, biogeography and the global flows of alien amphibians and reptiles. Diversity & Distributions 23(11): 1313–1322. https://doi.org/10.1111/ddi.12617

Caves EM, Jennings SB, Hille Ris Lambers J, Tewksbury J, Rogers HS (2013) Natural experiment demonstrates that bird loss leads to cessation of dispersal of native seeds from intact to degraded forests. PLoS ONE 8(5): e65618. https://doi.org/10.1371/journal.pone.0065618

Chiszar D (1990) The behavior of the brown treesnake: a study in applied comparative psychology. In: Dewsbury DA (Ed.) Contemporary Issues in Comparative Psychology. Sinauer Associates, Inc., Sunderland, 101–123. https://doi.org/10.1037/11525-005

Christy MT, Yackel Adams AA, Rodda GH, Savidge JA, Tyrrell CL (2010) Modelling detection probabilities to evaluate management and control tools for an invasive species. Journal of Applied Ecology 47(1): 106–113. https://doi.org/10.1111/j.1365-2664.2009.01753.x

Christy MT, Savidge JA, Yackel Adams AA, Gragg JE, Rodda GH (2017) Experimental landscape reduction of wild rodents increases movements in the invasive brown treesnake (*Boiga irregularis*). Management of Biological Invasions: International Journal of Applied Research on Biological Invasions 8(4): 455–467. https://doi.org/10.3391/mbi.2017.8.4.01

Clark L, Savarie PJ (2012) Efficacy of aerial broadcast baiting in reducing brown treesnake numbers. Human-Wildlife Interactions 6: 212–221. https://www.jstor.org/stable/24874095

Clark L, Savarie PJ, Shivik JA, Breck SW, Dorr BS (2012) Efficacy, effort, and cost comparisons of trapping and acetaminophen baiting for control of brown treesnakes on Guam. Human-Wildlife Interactions 6: 222–236. https://www.jstor.org/stable/24874096

Clark L, Clark C, Siers S (2018) Brown Treesnakes: Methods and approaches for control. In: Pitt WC, Beasley JC, Witmer GW (Eds) Ecology and Management of Terrestrial Vertebrate Invasive Species in the United States. CRC Press, Boca Raton, 107–134. https://doi.org/10.1201/9781315157078

Clout MN, Williams PA (2009) Invasive species management: a handbook of principles and techniques. Oxford University Press, Oxford. https://doi.org/10.1093/oso/9780199216321.001.0001

Deso G, Probst JM (2007) *Lycodon aulicus* Linnaeus, 1758 et son impact sur l'herpétofaune insulaire à La Réunion (Ophidia: Colubridae: Lycodontinae). Bulletin Phaeton 25: 29–36.

DIISE (2023) The Database of Island Invasive Species Eradications: developed by Island Conservation, Coastal Conservation Action Laboratory UCSC, IUCN SSC Invasive Species Specialist Group, University of Auckland and Landcare Research, New Zealand. http://diise.islandconservation.org

Dorr BS, Clark CS, Savarie PJ (2016) Aerial application of acetaminophen-treated baits for control of brown tree snakes (RC-200925; NWRC Study Number: QA-1828). Final Report, US-Department of Defense ESTCP.

Durso AM, Willson JD, Winne CT (2011) Needles in haystacks: Estimating detection probability and occupancy of rare and cryptic snakes. Biological Conservation 144(5): 1508–1515. https://doi.org/10.1016/j.biocon.2011.01.020

Engeman RM, Linnell MA (1998) Trapping strategies for deterring spread of brown tree snakes from Guam. Pacific Conservation Biology 4: 348–353. https://doi.org/10.1071/PC980348

Engeman RM, Shiels AB, Clark CS (2018) Objectives and integrated approaches for the control of brown tree snakes: An updated overview. Journal of Environmental Management 219: 115–124. https://doi.org/10.1016/j.jenvman.2018.04.092

Fosberg R (1960) The vegetation of Micronesia 1. General descriptions, the vegetation of the Marianas Islands, and a detailed consideration of the vegetation of Guam. Bulletin of the American Museum of Natural History 119: 1–1.

Freedman MG, Miller RH, Rogers HS (2018) Landscape-level bird loss increases the prevalence of honeydew-producing insects and non-native ants. Oecologia 188(4): 1263–1272. https://doi.org/10.1007/s00442-018-4273-5

Fricke EC, Tewksbury JJ, Rogers HS (2014) Multiple natural enemies cause distance-dependent mortality at the seed-to-seedling transition. Ecology Letters 17(5): 593–598. https://doi.org/10.1111/ele.12261

Fritts TH (1988) The Brown Tree Snake, *Boiga irregularis*, a Threat to Pacific Islands. US Department of Interior, Fish and Wildlife Service, Research and Development, Honolulu, 36 pp.

Fritts TH (2002) Economic costs of electrical system instability and power outages caused by snakes on the island of Guam. International Biodeterioration & Biodegradation 49(2–3): 93–100. https://doi.org/10.1016/S0964-8305(01)00108-1

Fritts TH, McCoid MJ (1991) Predation by the brown tree snake, *Boiga irregularis*, on poultry and other domesticated animals in Guam. Snake 23: 75–80.

Fritts TH, Rodda GH (1998) The role of introduced species in the degradation of island ecosystems: A case history of Guam. Annual Review of Ecology and Systematics 29(1): 113–140. https://doi.org/10.1146/annurev.ecolsys.29.1.113

Fritts TH, McCoid MJ, Haddock RL (1990) Risks to infants on Guam from bites of the Brown Tree Snake (*Boiga irregularis*). The American Journal of Tropical Medicine and Hygiene 42(6): 607–611. https://doi.org/10.4269/ajtmh.1990.42.607

Fritts TH, McCoid MJ, Haddock RJ (1994) Symptoms and circumstances associated with bites by the brown tree snake (Colubridae: *Boiga irregularis*) on Guam. Journal of Herpetology 28(1): 27–33. https://doi.org/10.2307/1564676

Genovesi P (2001) Guidelines for eradication of terrestrial vertebrates: A European contribution to the invasive alien species issue. Convention on the Conservation of European Wildlife and Natural Habitats 24: 1–28.

Goetz SM, Yackel Adams AA, Siers SR (2020) Validating deployment of aerially-delivered toxic bait cartridges for control of invasive brown treesnakes. Wildlife Society Bulletin 44(3): 617–622. https://doi.org/10.1002/wsb.1106

Goetz SM, Hileman ET, Nafus MG, Yackel Adams AA, Bryant A, Reed RN, Siers SR (2021) Brown treesnake mortality after aerial application of toxic baits. The Journal of Wildlife Management 85(7): 1507–1514. https://doi.org/10.1002/jwmg.22108

Gragg JE, Rodda GH, Savidge JA, White GC, Dean-Bradley K, Ellingson AR (2007) Response of brown treesnakes to reduction of their rodent prey. The Journal of Wildlife Management 71(7): 2311–2317. https://doi.org/10.2193/2006-444

Guam Department of Agriculture (2020) Invasive brown treesnake present on Cocos Island, agencies working to prevent further spread. Press release. Guam Department of Agriculture, Mangilao, 2 pp.

Hall TC (1996) Operational control of the brown tree snake on Guam. In: Timm R, Crabb AC (Eds) Proceedings of the 17th Vertebrate Pest Conference, March 1996. University of California, Davis, 234–240.

Johnston JJ, Savarie PJ, Primus TM, Eisemann JD, Hurley JC, Kohler DJ (2002) Risk assessment of an acetaminophen baiting program for chemical control of brown tree snakes on Guam: Evaluation of baits, snake residues, and potential primary and secondary hazards. Environmental Science & Technology 36(17): 3827–3833. https://doi.org/10.1021/es015873n

Kimball BA, Stelting SA, McAuliffe TW, Stahl RS, Garcia RA, Pitt WX (2016) Development of artificial bait for brown treesnake suppression. Biological Invasions 18(2): 359–369. https://doi.org/10.1007/s10530-015-1031-z

Klug PE, Yackel Adams AA, Reed RN (2021a) Olfactory lures in predator control do not increase predation risk to birds in areas of conservation concern. Wildlife Research 49(2): 183–192. https://doi.org/10.1071/WR21022

Klug PE, Yackel Adams AA, Siers SR, Brindock KM, Mazurek MJ, Mosher SM, Pitt WC, Reed RN (2021b) Locally abundant, endangered Mariana Swiftlets impact the abundance, behavior, and body condition of an invasive predator. Oecologia 195(4): 1083–1097. https://doi.org/10.1007/s00442-021-04876-0

Kraus F (2009) Alien reptiles and amphibians: A scientific compendium and analysis. Invading Nature-Springer Science & Business Media 4: 1–563. https://doi.org/10.1007/978-1-4020-8946-6

Kraus F (2015) Impacts from invasive reptiles and amphibians. Annual Review of Ecology, Evolution, and Systematics 46(1): 75–97. https://doi.org/10.1146/annurev-ecolsys-112414-054450

Lardner B, Savidge JA, Rodda GH, Reed RN (2009) Prey preferences and prey acceptance in juvenile Brown Treesnakes (*Boiga irregularis*). Herpetological Conservation and Biology 4(3): 313–323.

Lardner B, Yackel Adams AA, Savidge JA, Rodda GH, Reed RN, Clark CS (2013) Effectiveness of bait tubes for Brown Treesnake control on Guam. Wildlife Society Bulletin 37(3): 664–673. https://doi.org/10.1002/wsb.297

Lardner B, Yackel Adams AA, Savidge JA, Reed RN (2019b) Optimizing walking pace to maximize snake detection rate: A visual encounter survey experiment. Herpetologica 75(3): 218–223. https://doi.org/10.1655/D-18-00020

Lardner B, Yackel Adams AA, Knox AJ, Savidge JA, Reed RN (2019a) Do observer fatigue and taxon bias compromise visual encounter surveys for small vertebrates? Wildlife Research 46(2): 127–135. https://doi.org/10.1071/WR18016

Lindberg AC, Shivik JA, Clark L (2000) Mechanical mouse lure for brown treesnakes. Copeia 2000(3): 886–888. https://doi.org/10.1643/0045-8511(2000)000[0886:MMLFBT]2.0.CO;2

Mackessy SP, Sixberry NM, Heyborne WH, Fritts T (2006) Venom of the Brown Treesnake, *Boiga irregularis*: Ontogenetic shifts and taxa-specific toxicity. Toxicon 47(5): 537–548. https://doi.org/10.1016/j.toxicon.2006.01.007

Mathies T, Scarpino R, Levine BA, Clark C, Savidge JA (2011) Excluding nontarget species from Brown Tree Snake, *Boiga irregularis* (Reptilia: Colubridae), bait stations: Experimental tests of station design and placement. Pacific Science 65(1): 41–57. https://doi.org/10.2984/65.1.041

Mauldin RE, Savarie PJ (2010) Acetaminophen as an oral toxicant for Nile monitor lizards (*Varanus niloticus*) and Burmese pythons (*Python molurus bivittatus*). Wildlife Research 37(3): 215–222. https://doi.org/10.1071/WR08168

Medina S, Aguon C (2000) Establishment of an experimental population of Guam rails on Rota or other Northern Mariana Islands. In: Davis GW, Pitlik TJ, Leberer T, Vice D (Eds)

Annual Report Fiscal Year 2000, Division of Aquatic and Wildlife Resources, Guam Department of Agriculture, Mangilao, 174–183.

Monzón-Argüello C, Patiño-Martínez C, Christiansen F, Gallo-Barneto R, Cabrera-Pérez MÁ, Peña-Estévez MÁ, López-Jurado LF, Lee PLM (2015) Snakes on an island: Independent introductions have different potentials for invasion. Conservation Genetics 16(5): 1225–1241. https://doi.org/10.1007/s10592-015-0734-0

Nafus MG, Yackel Adams AA, Klug PE, Rodda GH (2018) Habitat type and structure affect trap capture success of an invasive snake across variable densities. Ecosphere 9(8): e02339. https://doi.org/10.1002/ecs2.2339

Nafus MG, Yackel Adams AA, Boback SM, Siers SR, Reed RN (2020) Behavior, size, and body condition predict susceptibility to management and reflect post-treatment frequency shifts in an invasive snake. Global Ecology and Conservation 21: e00834. https://doi.org/10.1016/j.gecco.2019.e00834

Nafus MG, Xiong PX, Paxton EH, Yackel Adams AA, Goetz SM (2021) Foraging behavior in a generalist snake (brown treesnake, *Boiga irregularis*) with implications for avian reintroduction and recovery. Applied Animal Behaviour Science 243: e105450. https://doi.org/10.1016/j.applanim.2021.105450

Nafus MG, Siers SR, Levine BA, Quiogue ZC, Yackel Adams AA (2022) Demographic response of brown treesnakes to extended population suppression. The Journal of Wildlife Management 86(1): e22136. https://doi.org/10.1002/jwmg.22136

Nafus MG, Collins AF, Viernes M, Hopkins C, Nacpil A (2023) Guam, USGS Closed Population (NWFN), an experimental eradication of brown treesnakes in a 5-ha study site, 2016 – 2023: US Geological Survey data release. https://doi.org/10.5066/P9QRWKQB

Nelson Jr L, Clark FW (1973) Correction for sprung traps in catch/effort calculations of trapping results. Journal of Mammalogy 54(1): 295–298. https://doi.org/10.2307/1378903

Perry G, Morton JM (1999) Regeneration rates of the woody vegetation of Guam's Northwest Field following major disturbance: Land use patterns, feral ungulates, and cascading effects of the brown treesnake. Micronesica 32: 125–142.

Perry G, Vice D (2009) Forecasting the risk of brown tree snake dispersal from Guam: A mixed transport-establishment model. Conservation Biology 23(4): 992–1000. https://doi.org/10.1111/j.1523-1739.2009.01169.x

Perry G, Pierce J, Griffin D, van Buurt G, Lazell J (2003) Geographic distribution: *Elaphe guttata guttata*. Herpetological Review 34: e264.

Pollock HS, Savidge JA, Kastner M, Seibert TF, Jones TM (2019) Pervasive impacts of invasive brown treesnakes drive low fledgling survival in endangered Micronesian Starlings (*Aplonis opaca*) on Guam. The Condor 121(2): duz014. https://doi.org/10.1093/condor/duz014

Pollock HS, Kastner M, Wiles GJ, Thierry H, Dueñas LB, Paxton EH, Suckow NM, Quitugua J, Rogers HS (2021) Recent recovery and expansion of Guam's locally endangered Såli (Micronesian Starling) *Aplonis opaca* population in the presence of the invasive brown treesnake. Bird Conservation International 32(1): 95–110. https://doi.org/10.1017/S0959270920000726

R Core Team (2021) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Reed RN, Kraus F (2010) Invasive reptiles and amphibians: Global perspectives and local solutions. Animal Conservation 13(s1, Supplement 1): 3–4. https://doi.org/10.1111/j.1469-1795.2010.00409.x

Reed RN, Tucker AD (2012) Determining age, sex, and reproductive condition. In: McDiarmid RW, Foster MS, Guyer C, Gibbons JW, Chernoff N (Eds) Reptile Biodiversity: Standard Methods for Inventory and Monitoring. University of California Press, Berkeley, 51–63.

Richmond JQ, Wood DA, Stanford JW, Fisher RN (2015) Testing for multiple invasion routes and source populations for the invasive brown treesnake (*Boiga irregularis*) on Guam: implications for pest management. Biological Invasions 17: 337–349. https://doi.org/10.1007/s10530-014-0733-y

Rodda GH, Fritts TH (1992) The impact of the introduction of the colubrid snake *Boiga irregularis* on Guam's lizards. Journal of Herpetology 26(2): 166–174. https://doi.org/10.2307/1564858

Rodda GH, Reed RN (2007) Size-based trends and management implications of microhabitat utilization by Brown Treesnakes, with emphasis on juvenile snakes. In: Witmer G, Pitt WC, Fagerstone KA (Eds) Managing Vertebrate Invasive Species: Proceedings of an International Symposium, Fort Collins (Colorado), August 2007. USDA/APHIS/WS, National Wildlife Research Center, Colorado, 257–267.

Rodda GH, Savidge JA (2007) Biology and impacts of Pacific island invasive species. 2. *Boiga irregularis*, the brown tree snake (Reptilia: Colubridae). Pacific Science 61(3): 307–324. https://doi.org/10.2984/1534-6188(2007)61[307:BAIOPI]2.0.CO;2

Rodda GH, Fritts TH, Chiszar D (1997) The disappearance of Guam's wildlife. Bioscience 47(9): 565–574. https://doi.org/10.2307/1313163

Rodda GH, McCoid MJ, Fritts TH, Campbell EW (1999a) 17. Population trends and limiting factors in *Boiga irregularis*. In: Rodda GH, Sawai Y, Chiszar D, Tanaka H (Eds) Problem Snake Management: The Habu and the Brown Treesnake. Cornell University Press, Ithaca, 236–254. https://doi.org/10.7591/9781501737688-025

Rodda GH, Fritts TH, Clark CS, Gotte SW, Chiszar D (1999b) A state-of-the-art trap for the Brown Treesnake. In: Rodda GH, Sawai Y, Chiszar D, Tanaka H (Eds) Problem Snake Management: The Habu and the Brown Treesnake. Cornell University Press, Ithaca, 268–305. https://doi.org/10.7591/9781501737688-029

Rodda GH, Savidge JA, Tyrrell CL, Christy MY, Ellingson AR (2007) Size bias in visual searches and trapping of brown treesnakes on Guam. The Journal of Wildlife Management 71(2): 656–661. https://doi.org/10.2193/2005-742

Rogers HS (2011) The fate of a silent forest: the effects of complete bird loss on the forest of Guam. PHD Dissertation, University of Washington, Seattle, Washington.

Rogers H (2020) Natural history of a silent forest. Journal of Natural History Education and Experience 14: 22–26.

Rogers HS, Hille Ris Lambers J, Miller R, Tewksbury JJ (2012) 'Natural experiment' demonstrates top-down control of spiders by birds on a landscape level. PLoS ONE 7(9): e43446. https://doi.org/10.1371/journal.pone.0043446

Savarie PJ, Clark L (2006) Evaluation of bait matrices and chemical lure attractants for brown tree snakes. In: Timm RM, O'Brien JM (Eds) Proceedings of the 22nd Vertebrate

Pest Conference, October 2006. University of California, Davis, 483–488. https://doi.org/10.5070/V422110077

Savarie PJ, York DL, Hurley JC, Volz S (2000) Testing the dermal and oral toxicity of selected chemicals to brown treesnakes. In: Salmon TP, Crabb AC (Eds) Proceedings of the 19th Vertebrate Pest Conference, March 2009. University of California, Davis, 139–145. https://doi.org/10.5070/V419110219

Savarie PJ, Shivik JA, White GC, Hurley JC, Clark L (2001) Use of acetaminophen for large-scale control of brown treesnakes. The Journal of Wildlife Management 65(2): 356–365. https://doi.org/10.2307/3802916

Savidge JA (1987) Extinction of an island forest avifauna by an introduced snake. Ecology 68(3): 660–668. https://doi.org/10.2307/1938471

Savidge JA (1988) Food habits of *Boiga irregularis*, an introduced predator on Guam. Journal of Herpetology 22(3): 275–282. https://doi.org/10.2307/1564150

Shivik JA (1998) Brown treesnake response to visual and olfactory cues. The Journal of Wildlife Management 62(1): 105–111. https://doi.org/10.2307/3802268

Shivik JA (1999) Carrion, context and lure development: The relative importance of sensory modalities to foraging brown tree snakes (*Boiga irregularis*). PHD Disseretation. Colorado State University, Fort Collins, Colorado.

Shivik JA, Clark L (1997) Carrion seeking in brown tree snakes: Importance of olfactory and visual cues. The Journal of Experimental Zoology 279(6): 549–553. https://doi.org/10.1002/(SICI)1097-010X(19971215)279:6<549::AID-JEZ2>3.0.CO;2-N

Shivik JA, Clark L (1999) Ontogenetic shifts in carrion attractiveness to brown tree snakes (*Boiga irregularis*). Journal of Herpetology 33(2): 334–336. https://doi.org/10.2307/1565737

Shivik JA, Bourassa J, Donnigan SN (2000) Elicitation of brown treesnake predatory behavior using polymodal stimuli. The Journal of Wildlife Management 64(4): 969–975. https://doi.org/10.2307/3803206

Shwiff SA, Gebhardt K, Kirkpatrick KN, Shwiff SS (2010) Potential economic damage from introduction of Brown Tree Snakes, *Boiga irregularis* (Reptilia: Colubridae), to the islands of Hawai'i. Pacific Science 64(1): 1–10. https://doi.org/10.2984/64.1.001

Siers SR (2015) Microgeographic and ontogenetic variability in the ecology of invasive Brown Treesnakes on Guam, and effects of roads on their landscape-scale movements. PHD Thesis. Colorado State University, Fort Collins, Colorado.

Siers SR (2021) Allometric regression of snake body length from head image measurements. Wildlife Society Bulletin 45(3): 538–545. https://doi.org/10.1002/wsb.1213

Siers SR, Savidge JA, Demeulenaere E (2017a) Restoration Plan for the Habitat Management Unit, Naval Support Activity Andersen, Guam. Prepared for Naval Facilities Engineering Command. Colorado State University, Fort Collins, 238 pp.

Siers SR, Savidge JA, Reed RN (2017b) Quantile regression of microgeographic variation in population characteristics of an invasive vertebrate predator. PLoS ONE 12(6): e0177671. https://doi.org/10.1371/journal.pone.0177671

Siers SR, Yackel Adams AA, Reed RN (2018a) Behavioral differences following ingestion of large meals and consequences for management of a harmful invasive snake: A field experiment. Ecology and Evolution 8(20): 10075–10093. https://doi.org/10.1002/ece3.4480

Siers SR, Dorr BS, Shiels AB, Chlarson FM, Macaoay LG, Mundo RM, Rabon JAB, Volsteadt RM, Hall MA, Clark CS, Mosher SM, Savarie PJ (2018b) Assessment of Brown Treesnake activity and bait take following large-scale snake suppression in Guam. USDA, APHIS, WS, National Wildlife Research Center Final Report QA-2438: 1–10.

Siers SR, Pitt WC, Eisemann JD, Clark L, Shiels AB, Clark CS, Gosnell RJ, Messaros MC (2019a) An automated bait manufacturing and aerial delivery system for landscape-scale control of invasive Brown Treesnakes on Guam. In: Veitch CR, Clout MN, Martin AR, Russell JC, West CJ (Eds) Island invasives: Scaling up to meet the challenge, Occasional Paper SSC 62. Gland, 348–355. https://doi.org/10.2305/IUCN.CH.2019.SSC-OP.62.en

Siers SR, Shiels AB, Payne CG, Chlarson FM, Clark CS, Mosher SM (2019b) Photographic validation of target versus nontarget take of brown treesnake baits. Wildlife Society Bulletin 43(4): 752–759. https://doi.org/10.1002/wsb.1023

Siers SR, Shiels AB, Barnhart PD (2020a) Invasive snake activity before and after automated aerial baiting. The Journal of Wildlife Management 84(2): 256–267. https://doi.org/10.1002/jwmg.21794

Siers SR, Eisemann JD, Pitt WC, Clark L, Goetz SM, Gosnell RJ, Collins AF, Hileman ET, Nafus MG, Yackel Adams AA, Messaros MC, Coon WGN (2020b) Automated aerial baiting for invasive Brown Treesnake control: System overview and program status. In: Woods DM (Ed.) Proceedings of the 29th Vertebrate Pest Conference, Santa Barbara, California, March 2020: 1–7.

Siers SR, Goetz SM, Volsteadt RM, Nafus MG (2021) Evaluating lethal toxicant doses for the largest individuals of an invasive vertebrate predator with indeterminate growth. Management of Biological Invasions: International Journal of Applied Research on Biological Invasions 12(2): 476–494. https://doi.org/10.3391/mbi.2021.12.2.17

Silva-Rocha I, Salvi D, Sillero N, Mateo JA, Carretero MA (2015) Snakes on the Balearic Islands: An invasion tale with implications for native biodiversity conservation. PLoS ONE 10(4): e0121026. https://doi.org/10.1371/journal.pone.0121026

Stanford JW, Rodda GH (2007) The Brown Treesnake Rapid Response Team. In: Witmer G, Pitt WC, Fagerstone KA (Eds) Managing Vertebrate Invasive Species: Proceedings of an International Symposium, Fort Collins (Colorado), August 2007. USDA/APHIS/WS, National Wildlife Research Center, Colorado, 175–217.

Tonge S (1990) The past, present and future of the herpetofauna of Mauritius. Bulletin of the Chicago Herpetological Society 25: 220–226.

Tyrrell CL, Christy MT, Rodda GH, Yackel Adams AA, Ellingson AR, Savidge JA, Dean-Bradley K, Bischof R (2009) Evaluation of trap capture in a geographically closed population of brown tree snakes on Guam. Journal of Applied Ecology 46(1): 128–135. hhttps://doi.org/10.1111/j.1365-2664.2008.01591.x

U.S. Geological Survey (2023) Cocos Island, Guam Brown Treesnake rapid response visual survey and capture data, 10/2020–05/2023. U.S. Geological Survey data release. https://doi.org/10.5066/P9MT1JNO

USDA Wildlife Services (2009) Cocos Island biosecurity plan. Prepared by U. S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services. Barrigada, Guam.

USDA Wildlife Services (2021a) Biological Assessment for invasive Brown Treesnake eradication to protect natural resources on Cocos Island, Guam. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services. Barrigada, Guam.

USDA Wildlife Services (2021b) Cocos Island, Guam Brown Treesnake eradication. Draft Environmental Assessment. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services. Barrigada, Guam.

USFWS (2019) Species report for Slevin's Skink (*Emoia slevini*) – Final draft. U. S. Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office. Honolulu.

van den Hurk P, Kerkkamp HM (2019) Phylogenetic origins for severe acetaminophen toxicity in snake species compared to other vertebrate taxa. Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology 215: 18–24. https://doi.org/10.1016/j.cbpc.2018.09.003

Vice DS, Engeman RM, Vice DL (2005) A comparison of three trap designs for capturing brown treesnakes on Guam. Wildlife Research 32(4): 355–359. https://doi.org/10.1071/WR04046

Weijola V, Vahtera V, Koch A, Schmitz A, Kraus F (2020) Taxonomy of Micronesian monitors (Reptilia: Squamata: Varanus): endemic status of new species argues for caution in pursuing eradication plans. Royal Society Open Science 7(5): e200092. https://doi.org/10.1098/rsos.200092

Wiles GJ (1987) The status of fruit bats on Guam. Pacific Science 41: 1–4.

Wiles GJ, Bart J, Beck Jr RE, Aguon CF (2003) Impacts of the brown tree snake: Patterns of decline and species persistence in Guam's avifauna. Conservation Biology 17(5): 1350–1360. https://doi.org/10.1046/j.1523-1739.2003.01526.x

Yackel Adams AA, Lardner B, Knox AJ, Reed RN (2018) Inferring the absence of an incipient population during a rapid response for an invasive species. PLoS ONE 13(9): e0204302. https://doi.org/10.1371/journal.pone.0204302

Yackel Adams AA, Nafus MG, Klug PE, Lardner B, Mazurek MJ, Savidge JA, Reed RN (2019) Contact rates with nesting birds before and after invasive snake removal: Estimating the effects of trap-based control. NeoBiota 49: 1–17. https://doi.org/10.3897/neobiota.49.35592

Yackel Adams AA, Barnhart PD, Rodda GH, Hileman ET, Nafus MG, Reed RN (2021) Can we prove that an undetected species is absent? Evaluating whether brown treesnakes are established on the island of Saipan using surveillance and expert opinion. Management of Biological Invasions: International Journal of Applied Research on Biological Invasions 12(4): 901–926. https://doi.org/10.3391/mbi.2021.12.4.09